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EFFECTS OF ACCELERATED SEA-LEVEL RISE ON COASTAL SECONDARY PRODUCTION

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Abstract

Sea-level rise alters biochemical processes and the geomorphology of coastal habitats when saltwater submerges marshes and uplands. This coastal inundation can change the way marshes function as estuarine habitats. One change can occur through increased abundance of marsh algae which stimulates production of primary consumers. When grazers in drowning marshes become more accessible to estuarine predators, greater production may result at higher trophic levels. But such changes are transitional, and the benefits can disappear when drowning marshes convert to open-water habitats without plants.

Our evidence indicates that marsh submergence on the order of 1 cm per year enhances utilization of food resources by shrimp and crab predators. The apparent near-term effect is that production of secondary consumers is increased, but the long-term effect is not clear. Since estuarine-dependent shrimp and blue crab fisheries are among the largest in the U.S., the consequences of sea-level rise affecting their productivity is a concern. Moreover, subsiding marshes may simulate effects of submergence by the sea, providing a model for predicting changes in fisheries attributable to sea-level rise from global warming.

Introduction

Recent investigations emphasize that access to marsh surfaces may greatly influence productivity of estuarine consumers. Previously, investigators noted that fishery

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species use marsh creeks (Weinstein 1979), marsh infauna are impacted by estuarine predators (Bell and Coull 1978), and some offshore fishery yields can be related to the amount of marsh area inshore (Turner 1977). But until development of drop trap (Zimmerman et al.1984) and flume (McIvor and Odum 1986) sampling methods, the extent of utilization of marsh surfaces by transient estuarine consumers was unknown. These studies revealed that large numbers of estuarine animals often directly invade tidal marshes (Zimmerman and Minello 1984; Rozas and Odum 1987; McIvor and Odum 1988; Hettler 1989; Mense and Wenner 1989) in densities exceeding those of subtidal habitat.

However, utilization of marsh surfaces by invading nekton differs regionally, with comparatively less exploitation (fewer animals per unit area) in East Coast marshes (Hettler 1989; Mense and Wenner 1989) than in Gulf Coast salt marshes (Zimmerman and Minello 1984; Thomas et al. 1990). The reasons behind regional differences are unclear, but tides, inundation patterns and marsh morphology are likely involved. Differences in tidal scaling, geophysical effects and marsh surface accretion rates can modify amplitude, frequency, and duration of tidal inundation patterns regionally (Provost 1976). These factors affect the time available to estuarine predators for exploitation of marshes and the quantity and quality of marsh prey.

Regional differences have been expressed in trophic dynamic terms, through indentification of carbon sources and food chain pathways. East Coast marshes are valued for outwelling of organic materials which fuel estuarine food chains (Odum 1980). Tracing of this organic carbon from marshes has been elusive and, to date, evidence that large energetic contributions of marsh detritus control estuarine food chains is not convincing (Pomeroy 1989). Stable isotope ratios reveal that algal carbon is at least equal to the vascular detritus carbon in food chains associated with East Coast salt marshes (Haines 1976; Peterson and Howarth 1987). In the Gulf of Mexico, Sullivan and Moncrief (1988a) demonstrated that edaphic algal production in marshes is higher than on the East Coast and propose (Sullivan and Moncrief 1988b) that more algal carbon is incorporated into food chains associated with Gulf estuaries. The algae and their grazers are common foods of juvenile shrimps and crabs (Gleason 1986; Thomas 1989; Stoner and Zimmerman, 1988; McTigue and Zimmerman, in press) and small fishes (Minello et al. 1989) which exploit marshes.

Thus, secondary production of estuaries can be

modified through production of algae in marshes and the accessibility of primary consumers. Primary consumers, such as amphipods and tanaidaceans (peracarid crustaceans) and annelid worms, are among the most abundant macroinvertebrate components of salt marshes (Thomas 1976; Kneib 1982; Rader 1984) and, as prey, these organisms may transfer energy to higher trophic levels. Accordingly, mechanisms which control availability of primary consumers to estuarine predators may greatly determine the degree of coupling between the marsh and secondary productivity.

It has been postulated that greater productivity occurs in juveniles of fishery species through increasing their access to high abundances of foods (mainly primary consumers) in marshes (Boesch and Turner 1984; Zimmerman and Minello 1984; Minello and Zimmerman in press). Childers et al .(1990) and Morris et al (1990) have related annual fluctuations in sea level to secondary productivity of fisheries, and Zimmerman and Minello (1984) have shown that fishery juveniles increase their utilization of marsh surfaces during periods of seasonally high water. However, specific investigations relating utilization of marsh surfaces by transient predators to abundances of resident marsh prey have not been conducted.

In this paper, we show predator-prey relationships between three transient predators and their prey on a marsh surface undergoing submergence. Marsh submergence is the mechanism which in this case increases prey availability and elicits a response in predation. The submergence rate of the marsh simulates a moderate increase in eustatic sea-level rise. The estuarine predators are brown shrimp (_Penaeus aztecus_), white shrimp (_P. setiferus_) and blue crab (_Callinectes sapidus_). The prey are macro-invertebrate peracarid crustaceans and annelid worms which are common temperate marsh infauna and epifauna.

Methods

The salt marsh described in this study, located on Galveston Island in the northwestern Gulf of Mexico, is the site of an investigation continuing since 1981 (the site is described in Zimmerman et al. 1984). The marsh is undergoing submergence at a rate which exceeds its ability to accrete and maintain its elevation above sea level. The result is a high degree of reticulation between marsh and open-water habitat, including a large amount of marsh to open-water edge, and inundation by flood tides for a relatively large percentage of time. The duration of flooding at the marsh edge ranges between 10 and 75 % of each month depending upon season and year (unpublished water level record data).

Densities of shrimp, crab and fish fauna, on the marsh surface and in open-water habitat adjoining the marsh, were measured using drop trap sampling (Zimmerman et al. 1984). Habitat along the outer marsh edge was subtidal nonvegetated mud bottom. Each habitat was sampled within 2 m of the marsh edge, and 8 samples were taken from each habitat monthly. The area enclosed by each sample was 2.6 m^2. Decapods and fishes larger than 5 mm length were removed, identified and enumerated. For predators in this paper, only brown shrimp, white shrimp and blue crab are considered.

To quantify densities of infauna and epifauna as food organisms (prey), substrate cores, 10 cm dia. x 5 cm deep, were taken from within each drop trap. Samples from the marsh surface included 6 to 8 culms of marsh (*Spartina alterniflora*) vegetation. Cores were sieved through a 500-micron screen to retain peracarids, molluscs and annelids. These small macrofauna were removed, identified and enumerated.

Marsh submergence was estimated using subsidence measured by land elevation changes at four USGS bench marks in the area of the Galveston Island State Park (data from the Harris-Galveston County Subsidence District in Friendswood, Texas). Seasonal, annual, and long-term changes in sea level for the greater area were obtained from a permanent NOAA tide station (No. 877-1450) in Galveston (data from Lyles et al. 1988).

This paper covers the period in 1985 beginning with the spring immigration of predators and ending with their fall emigration.

Animal Densities

Predaceous brown shrimp, white shrimp, and blue crab occurred in comparatively high densities on the marsh surface, and densities were usually significantly greater in the marsh than in nearby open water (Figure 1). Variation in monthly abundances followed predictable patterns of seasonal immigration. Brown shrimp occurred in highest abundance during spring recruitment, and white shrimp abundance peaked in the summer (described by Baxter and Renfro 1967).

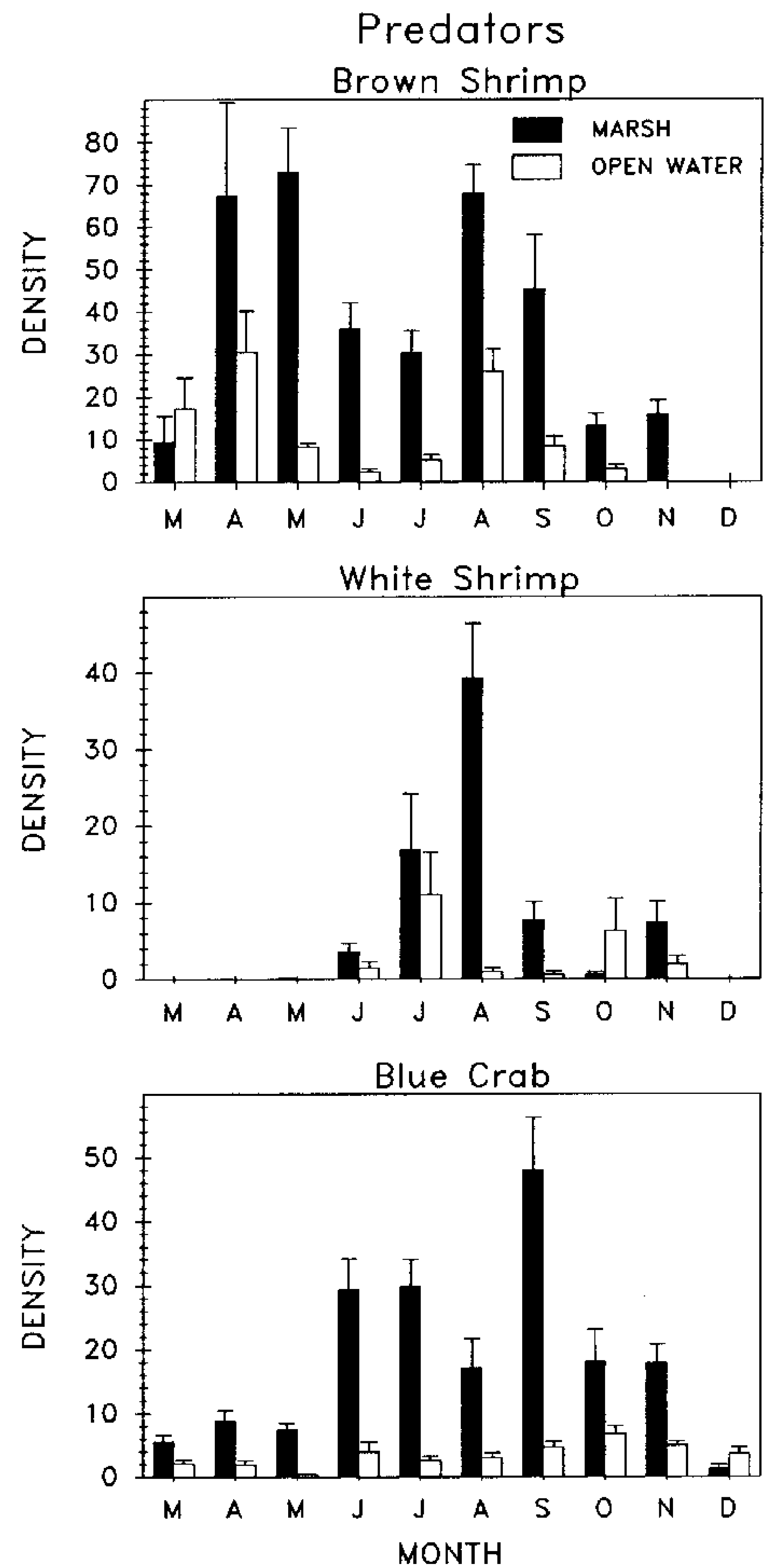

Figure 1. Densities (mean # per 2.6 $m^2 \pm 1$ SE) of decapod crustacea, as predators, on marsh surface and adjacent mud bottom, in a subsiding area of Galveston Bay.

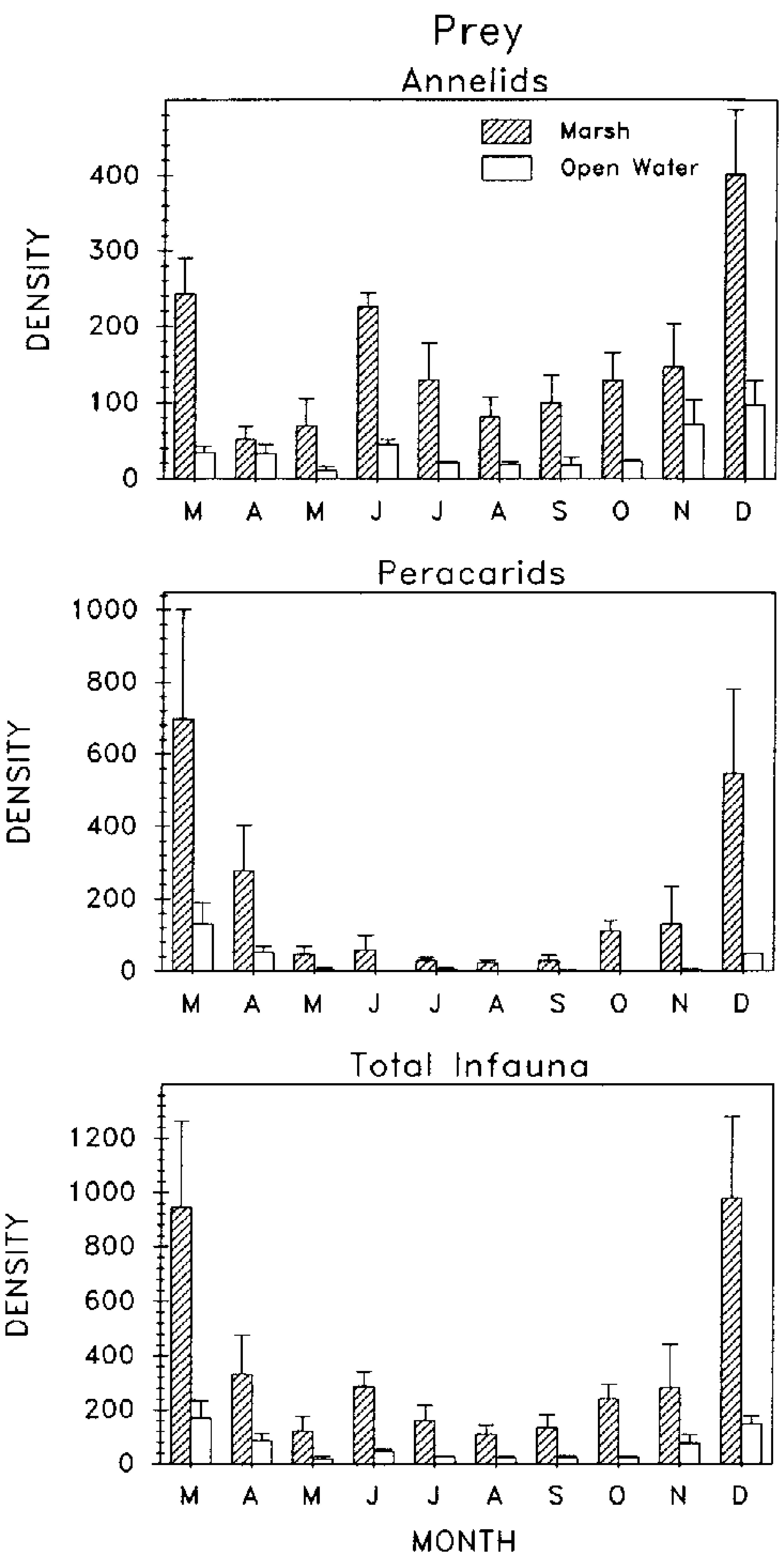

Figure 2. Densities (mean # per 78 cm^2 $\pm$1 SE) of infauna, as prey, on the marsh surface and adjacent mud bottom, in a subsiding area of Galveston Bay.

Blue crabs recruited in large numbers in the fall (Thomas et al. 1989).

The infauna and epifauna, as prey, were most abundant in the winter and early spring and least abundant from late spring to late fall (Figure 2). Mean prey densities were often several times higher in the marsh, in association with marsh plants, as compared to open-water habitat.

Predator-Prey Relationships

Predators entered the marsh system beginning in the spring, as represented by immigration of brown shrimp, and continued through the summer and fall, as represented by immigration of white shrimp and blue crabs. Peak abundances of all predators combined occurred during the summer and early fall before the onset of fall emigration. Thus, maximum predation pressure occurred during the warm months (Figure 1). The winter season was virtually free of effects of large numbers of predators.

The effects of predation are evident in the seasonal changes in prey populations. Populations of infauna build to peak abundances during March and April, and then decline sharply by May (Figure 2). The rapid decline suggests a cropping effect by predators. Throughout the warm months, infaunal populations were subjected to the heaviest predation, but their densities remained relatively stable. This indicates that prey populations can maintain themselves at lower levels and suggests that consequent production is largely going to the predators. The pattern of predation appears to be similar in peracarids and annelids.

Previous field caging studies and manipulative experiments have established that peracarids and annelids are important prey to juvenile penaeid shrimp and blue crabs (Young et al. 1976; Nelson 1981; Leber 1985; Thomas 1989; Nelson and Capone 1990). Thus, responses of prey populations in our study can be attributed to effects of predation by decapod crustaceans and small fishes. Since shrimp and crab densities are several times greater than fish densities on the marsh surface (Zimmerman and Minello 1984), decapods may dominate as predators.

Habitat Value of the Marsh Surface

Marsh habitats are valuable for production of high densities of infauna and epifauna which are at least potentially available to aquatic consumers (Kneib 1982, 1984; Rader 1984; Fleeger 1985). These prey may be exported to subtidal habitats near the marsh edge or fed upon directly on the marsh surface. Our data suggest that predators may preferentially exploit marsh habitat because of the high prey abundances.

Marsh habitat also is valuable as refuge for the juveniles of transient estuarine species. The structure of marsh plants provides protection for juvenile shrimp and crabs against predation by fishes (Minello and Zimmerman 1983; Minello et al. 1989; Thomas 1989). Thus, survivorship of these decapods, as well as their impacts as predators, may be increased by greater access to marsh habitat (Minello et al. 1989; Minello and Zimmerman in press).

Sea-Level Change

Between 1960 and 1985, the cumulative increase in relative sea level at the Galveston Pier 21 NOAA tide gage was approximately 20 cm (Figure 3). The rate was about 8 mm per year (Paine 1990). Eustatic change in sea level over that period is assumed to be about 1 mm per year (Etkins and Epstein 1982; Gornitz et al. 1982) with the remainder due to land elevation changes at the tide gage. The record depicts occurrence of large annual fluctuations in relative sea-level, including some periods of rapid rise and other periods of sharp decline (Figure 3).

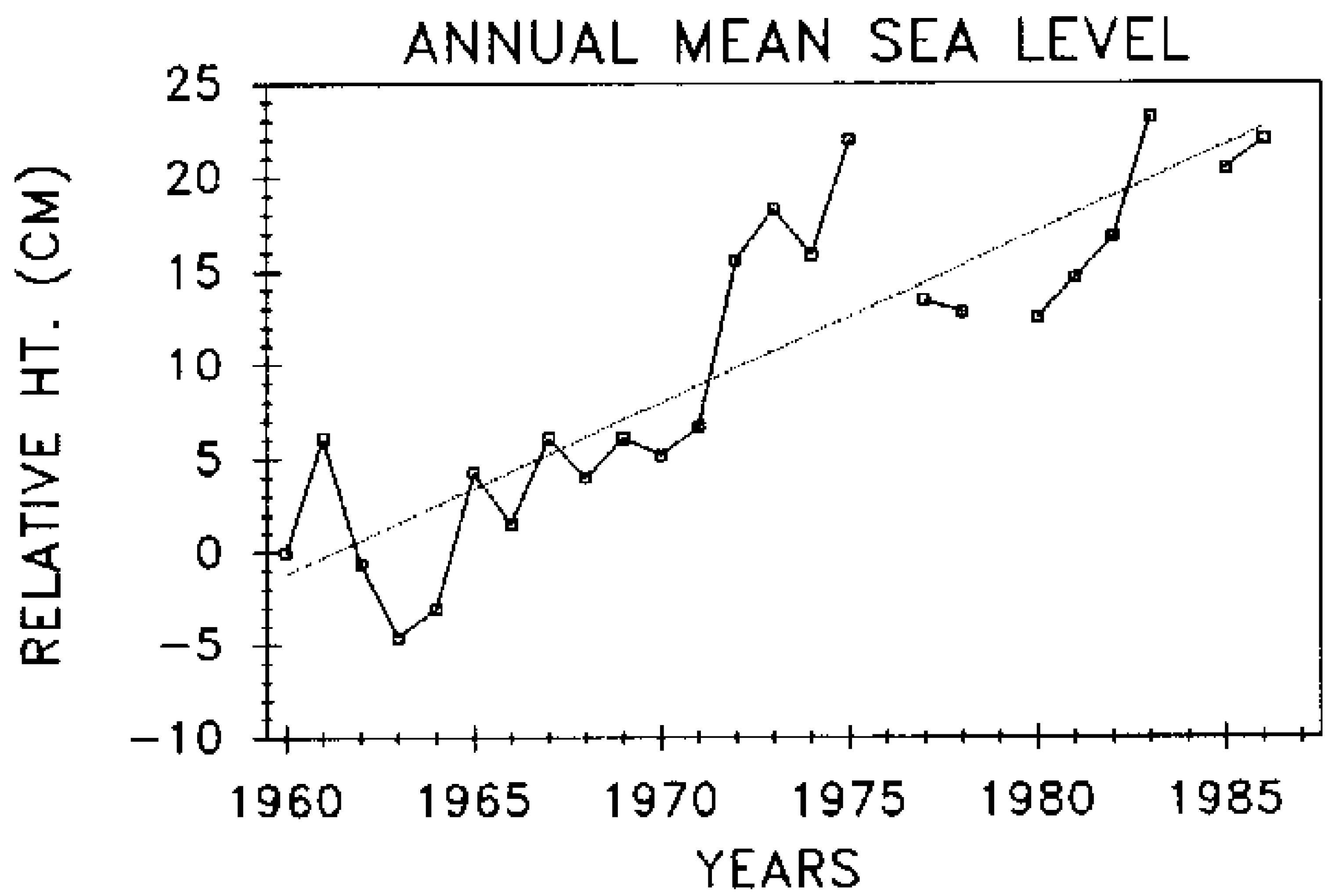

Figure 3. Annual mean changes in relative sea level at NOAA tide station No. 887-1450 on Galveston Island.

Marsh Submergence

Subsidence rates at the marsh site have been increasing at least since 1958 (Table 1; data from the Harris-Galveston County Subsidence District, Friendswood, Texas). Accordingly, land surfaces became lower by rates of 3.6, 7.4 and 13.7 mm per year between the intervals 1958-1964, 1964-1978 and 1978-1987, respectively. The subsidence rates plus eustatic sea-level rise provide an estimate of the marsh submergence and drowning rate. Since the marsh surface appears to be undergoing erosion rather than accretion, the estimated submergence rate may be understated. We note that submergence at the site is greater than that approximated by the Galveston NOAA tide gage, located about 20 km east of the marsh site.

Table 1. National Geodetic Survey bench marks (elevation in ft.) in the area of a salt marsh on Galveston Island.

Designation	1958	1964	1978	1987
J 1186	----	9.842	9.516	9.18
K 1186	----	4.091	3.775	3.42
Park R M 2	----	----	7.774	7.25
D 460	9.567	9.495	9.119	----

Flooding of the marsh surface varied monthly, following usual seasonal tide patterns for the northern Gulf of Mexico (Lyles et al. 1988). Seasonal tides cause prolonged inundation in the spring and fall and less inundation in the winter (Figure 4).

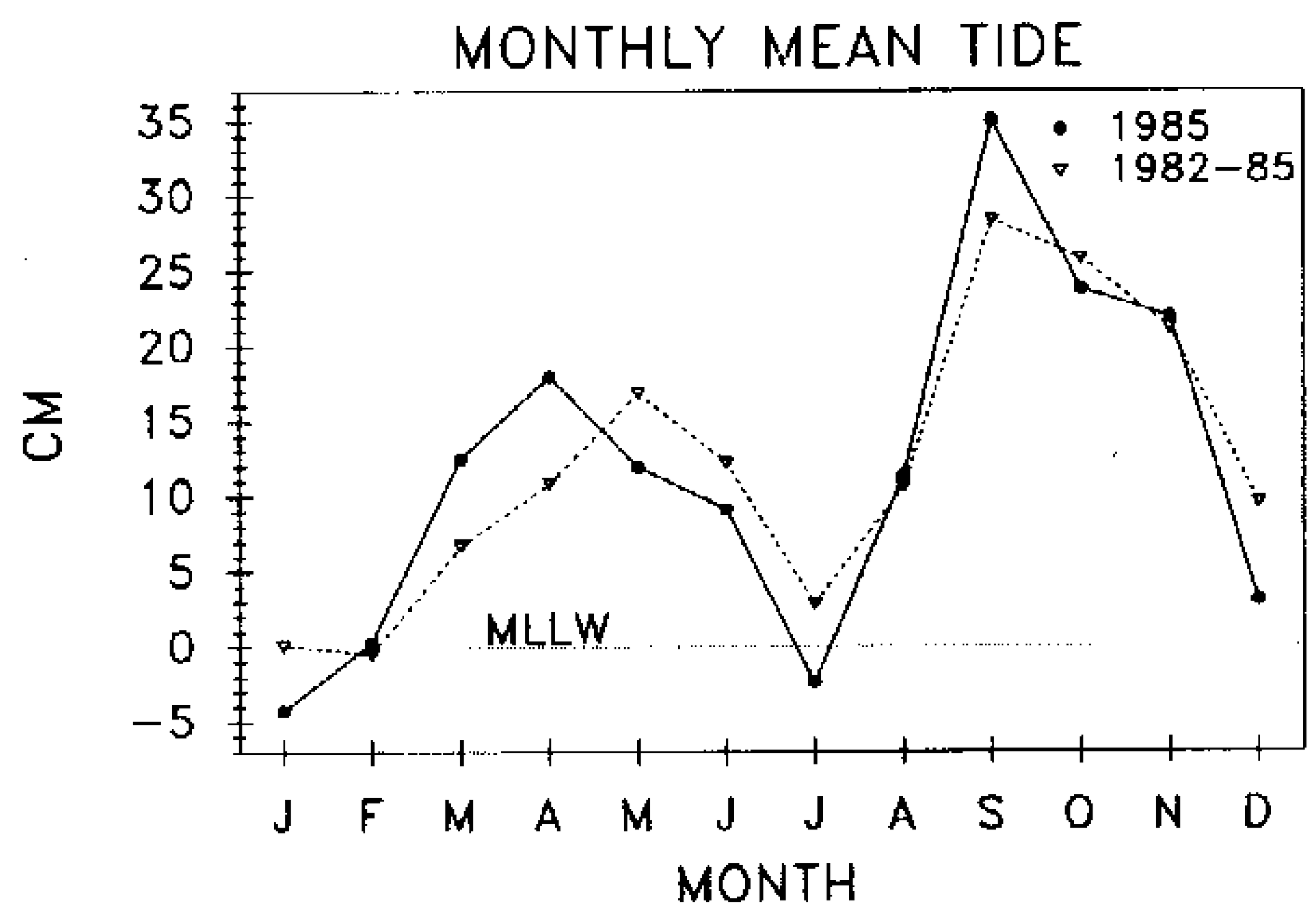

Figure 4. Monthly mean tide level changes at NOAA Station No. 887-1450 on Galveston Island.

Relationships Between Marsh Submergence and Habitat Value

The value of habitat, in terms of food and refuge, increases for consumers when marshes undergo submergence and prolonged inundation, extending the time and area available for exploitation. In the process of becoming more submerged, marsh plants also begin to die as they drown (Mendelssohn and McKee 1988), and thus eventually the marsh converts into open water. During the transition, a greater amount of marsh to open-water edge is created which further improves the accessibility of marshes to consumers. Decreasing plant density in drowning marshes may further accommodate ease of access.

Regional Differences

Compared to other regions, the number of estuarine animals using northwestern Gulf marshes is relatively high. The few density measurements from the East Coast of shrimp and blue crabs utilizing marshes (Hettler 1989; Mense and Wenner 1989) are orders of magnitude lower than those of the northwestern Gulf (Zimmerman and Minello 1984; Thomas et al. 1989). We propose that such differences reflect dissimilarity in the regional levels of secondary production derived directly from marshes.

Since land surface movements and scales of tides differ regionally, processes and functions of marshes may vary on a regional basis. East Coast marshes tend to have larger tidal amplitudes and less subsidence than northwestern Gulf marshes. Meso-scale tides promote exportation of marsh materials and importation of sediments, but may limit use of marsh surfaces to specialized organisms. Micro-scale tides can lessen transport of materials, but may promote the use of marsh surfaces by organisms. Marsh submergence, through subsidence or water-level rise, also can promote direct utilization by consumers. Increased utilization, such as is occurring in northwestern Gulf marshes, translates into more secondary production from marsh habitat. Less direct utilization of East Coast marshes by consumers may result in lower secondary production.

Implications of Marsh Submergence to Sea-Level Rise

Biological response patterns, including productivity and trophic dynamic responses, in submerging marshes provide a model for predicting effects of accelerated sea-level rise. For example, our evidence suggests that changes in coastal fisheries production can occur with accelerated sea-level rise. Productivity of estuarine-dependent fisheries may increase or decline because of the effects of sea-level rise on marsh function. The most immediate changes will occur in marsh areas with micro-tides and high subsidence rates. In particular, modifications to fishery productivity may be already underway in the northwestern Gulf of Mexico, where water-level changes are similar to those predicted by global warming/sea-level rise models.

Secondary production may increase, at least temporarily, in marshes undergoing submergence due to sea-level rise at rates of 5 to 10 mm per year. In this case, habitat function and utilization is improved for consumers due to greater inundation of marsh surfaces and to the relatively slow die-back of plants at the marsh edge. If salt marsh plants invade upland at the same rate as the outer edge decays (due to drowning), the overall area of the marsh is maintained.

Secondary production may decline sharply, however, when eustatic sea-level rise rates exceed 1 cm per year because rapidly drowning marshes may not be able to maintain habitat area. At some point in sea-level rise, inland re-establishment rates will not keep pace with the outer edge die-back. The loss of habitat in this case outweighs the improvement to habitat function for consumers. This scenario will almost assuredly occur in areas presently undergoing high rates of subsidence.

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